type over another (G=2.995, df=1, P=0.084). The average time to pick-up leaf A fragments was 13.8 ± 6.0 seconds (mean ± SE) and the average time to pick up of leaf B fragments was 9.8 ± 3.0 seconds. There was no significant difference between these times (t=0.916, df=7, P=0.390).

Ants on trail B did not pick up any leaf A fragments, but transported 10 of 10 leaf B fragments, showing a preference for B leaves (G=27.726, df=1, P<0.001). The average time to pick-up leaf B fragments was 16.8 ± 5.7 seconds.

DISCUSSION (VRL)

Since ants on trail A transported both A and B leaves, they did not follow our prediction that ants will only transport target leaves. However, ants on trail B did support our hypothesis. It is difficult to draw broad conclusions from our results since we only sampled two trails of a colony.

Tree A and B differed in their distance from the colony. Kunz et al. (1994) found that ants appeared to be more selective of the leaves they transported when they were at greater distances from the colony. This finding may help explain our results since tree B, where ants transported only B leaves, was three times as far from the colony as tree A, where ants transported both leaf types.

An alternative explanation is that *A. cephalotes* is optimizing the growth of the fungus by selecting leaves with a specific chemical composition or physical characteristics (Stevens 1983). If the fungus grows better on B leaves, the ants should prefer them over A leaves. Although ants on trail A showed no statistically significant preference for B leaves, the trend was that they picked up more B leaves and picked them up more quickly. In addition, ants on trail B never transported an A leaf.

Further study should examine multiple trails at several distances from a colony. In addition, further study might examine if leaf selectivity differs with distance or physical and chemical characteristics of the leaves.

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SIZE DISTRIBUTION AND HABITAT PREFERENCE IN HERMIT CRABS

SHARON D. KARLSBERG AND JOANNA M. HUBBARD

Abstract. (SDK) Hermit crabs are distributed in the intertidal zone, from the upper beach to outer tide pools, the pattern varying with the tidal cycle. Based on preliminary observations, we predicted that distribution along the intertidal gradient would vary among crab size classes. Distributional patterns and preference trials of large and medium crabs supported this hypothesis. Medium crabs selected dune edges over forest, which was preferred by large crabs. Additionally, factors such as heat stress and predator threat seem to direct hermit crabs to shaded, sheltered habitats. As hermit crabs can find shade and shelter in both dune edge and forest habitats, size class preferences for a particular area may be a mechanism to reduce intraspecific competition between crabs at low tide.

INTRODUCTION (JMH)

Hermit crab distribution varies with the tidal cycle (Dudycha et al. 1992). At high tide, most are found in the upper beach along the forest edge (Fenster and Lehmkuhl 1984, Dudycha et al. 1992). As more beach area is exposed, they become more evenly distributed across the intertidal gradient. Dudycha et al. (1992) suggested that at low tide large crabs occurred in greater numbers in the upper beach near the forest and high tide line, while small crabs were found more frequently further down the beach in tidal pools.

We examined hermit crab distribution on a Costa Rica beach. We hypothesized that: (1) crabs of different sizes would prefer different beach microhabitats, with large crabs occurring disproportionately further up the beach than smaller size classes; (2) different size crabs would show a preference for certain habitat characteristics (food availability, refuge from predators, or relief from heat stress); and (3) preference will be less important in determining distribution of hermit crabs at high tide when the area of the beach is sharply decreased.

METHODS (SDK)

Crab distribution: We recorded the abundance of hermit crabs along three transects on the beach near the end of the Sirena Trail, Corcovado National Park, Costa Rica. We established three 100 m transects, 20 m apart, perpendicular to the edge of the forest. These were located on both sides of the trail exit beginning 1 m from the forest edge. Between 0900 and 0945 on 2 and 3 February 1995, we recorded the number of hermit crabs at low tide at 0 m and 1 m on the transect, then every 5 m from 5-50 m, and finally at 10 m intervals from 50-100 m, 17 sampling points in all. We measured all crabs within a 1.5 m^2 plot at each sampling point. Three size classes based on shell aperture width were recognized: large crabs, >10 mm; medium crabs, 7-10 mm; and small crabs, <7 mm. These transect data were then grouped by distance from the forest edge into five beach habitat categories: forest (<1 m), dune edge (1-<5 m), high tide area (5-<10 m), sandy beach (10-20 m), pebble sand (25-35 m), and tidal flats (40-100 m). The same transects were surveyed at high tide between 1415 and 1515 on 2 February 1995. Transects ran from the forest edge (0 m) to the water line (1-15 m) and were grouped as forest (<1 m) and beach (1-15 m).

Preference trials: Seven paired preference trials were performed with 10 large (L) and 10 medium (M) crabs. For each trial replicate, a naive crab (gathered from beach 25 m distant) was placed in the center of two side by side manipulated habitats. We set up trial habitats in a circular fashion, surrounding the test crab

with one habitat choice on either half of the circle, to minimize subject escape. Lastly, we randomized the direction each crab faced. If a test subject tried to escape both trial habitats (often the case), we would replace it with another. In all cases, we waited until a crab had remained in one particular preference habitat for at least 10 seconds; this habitat was then recorded as the subject's selected habitat.

Paired preference trials were as follows:

- T1 forest litter vs. high tide litter
- T2 shaded sand vs. exposed sand
- T3 shaded sand vs. shade + high tide litter (medium crabs); shaded sand vs. shade + forest litter (large crabs)
- T4 shaded sand vs. exposed sand + food forage
- T5 driftwood refuge vs. food forage (both shaded)
- T6 driftwood refuge vs. shaded sand
- T7 shade vs. driftwood refuge + food forage

We created trial habitats with minimal disturbance to the original beach habitat. Shaded habitats were created by positioning an umbrella over the sand. We transplanted forest litter (dried leaves, sticks, understory grasses) and high tide litter (few leaves, driftwood, coconut, rotting fruit, rock) onto our test site (mid-beach) to simulate the forest and high tide environments. We supplied large pieces of driftwood for refuge trials, and used rotting fruits, bananas, and pieces of crab legs as bait in food forage trials.

RESULTS (JMH)

Crab Distribuution. A G-test comparison on the frequency data for low tide showed a significant difference in the distribution between different beach habitats by crab size class (G=25.06, df=10, P=0.005). Based on deviation from expected values, the greatest non-random distribution of medium size class crabs was found in the edge and high tide habitats (in decreasing order of deviation). Large crabs had the greatest deviation from random distibution over the forest, edge, and high tide beach habitats (there was no difference in deviation from

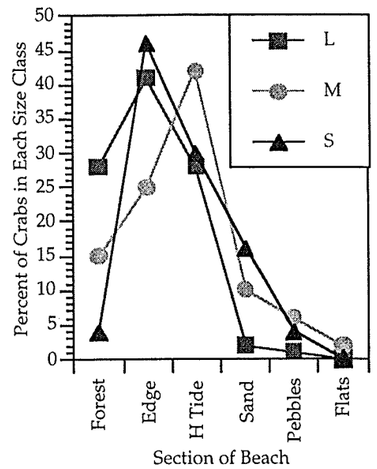

FIG. 1. Spatial pattern of the three size classes of hermit crab found in six sections of the beach during low tide. Forest is <1 m, Edge is 1-<5 m, High Tide Area is 5-<10 m, Sand is 10-20 m, Pebble is 25-35 m, Flats is 40-100 m; distance is from the forest at the top of the beach. Large size class crabs=L (n=125), medium size class crabs=M (n=223), small size class crabs=S (n=50).

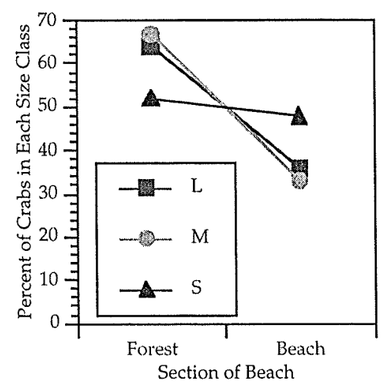

FIG. 2. Spatial pattern of the three size classes of hermit crabs found in two sections of the beach during high tide. Forest is <1 m and Beach is 1-15 m from the forest at the top of the beach. Large size class crabs=L (n=129), Medium size class crabs=M (n=205), Small size class crabs=S (n=54).

TABLE 1. Crab choice, by size class, among preference treatments in seven trials. Trials (T1-T7) examined the effect of heat stress, food availability, and predator refuge on habitat choice in hermit crabs. * indicates significant deviation from results predicted by random chance alone.

Trial Designation		Habitat 1	Habitat 2	P-value
Trial 1		**forest litter**	**high tide litter**	
Large	T1-L	8	2	0.04 *
Medium	T1-M	1	9	0.01 *
Trial 2		**shaded sand**	**exposed sand**	
Large	T2-L	8	2	0.04 *
Medium	T2-M	5	5	0.25
Trial 3		**shade**	**shade + litter**	
Large	T3-L	3	7	0.12
Medium	T3-M	6	4	0.21
Trial 4		**shade**	**food forage**	
Large	T4-L	6	4	0.21
Medium	T4-M	8	2	0.04 *
Trial 5		**driftwood refuge**	**food forage**	
Large	T5-L	5	5	0.25
Medium	T5-M	9	1	0.01 *
Trial 6		**driftwood refuge**	**shade**	
Large	T6-L	1	9	0.01 *
Medium	T6-M	4	6	0.21
Trial 7		**shade**	**refuge + food**	
Large	T7-L	5	5	0.25
Medium	T7-M	5	5	0.25

expected values among these four areas). At high tide, the observed distribution of crabs by size class in the avaliable habitats, 0 m to 15 m from the forest, did not deviate significantly from random (G=1.164, df=2, P=0.56). These data, converted into percentage of crabs in each size class in the different beach habitats for low and high tide, are shown in Figs. 1 and 2. Crab distribution at low tide varied by size class and habitat (Fig. 1). The highest proportion of large and small size class crabs at low tide were found 1 m from the forest (Edge, Fig. 1), while the highest proportion of medium size class crabs was found 5 m from the forest (High Tide, Fig. 1). At high tide, the highest proportion of crabs, for all three size classes, was found in the forest (Forest, Fig. 2).

Habitat Preference Trials. A binomial statistical test was performed on the results of the seven preference trials for two size classes of crab. The results (Table 1) indicate that large crabs selected forest litter over the high tide litter (T1-L). Conversely, medium-sized crabs selected high tide litter (T1-M). Large-size crabs also chose shade over refuge or open sand (T2-L and T6-L). Medium-sized crabs chose shade and refuge (in separate trials) over food (T4-M and T5-M). Other preference trials were inconclusive.

DISCUSSION (SDK)

Crab distribution. The data support the hypothesis that crabs of different sizes differentially distribute themselves across the intertidal gradient at low tide. Medium size crabs were non-randomly distributed at the dune edge and high tide line. The distribution data do not allow us to pinpoint the preferred microhabitat for large crabs, but they were also non-randomly distributed along the upper beach habitats (forest, dune edge, and high tide line). This indicates that at low tide, large and medium crabs occur at least partly in different beach microhabitats. At high tide, these non-random distribution trends disappear as dry beach area becomes reduced and all crabs forage in the upper habitats (forest and dune edge, Fig. 2). This daily tidal cycle thus ensures that crabs of different sizes may forage in specific upper beach habitats during low tides, but all crabs overlap in the forest

edge during high tide, which could lead to increased competition for food or shelter.

In our study of hermit crab habitat preference, small crabs were noticeably absent. When we did locate small crabs, it was usually out beyond the 100 m transect in a few shallow tidal pools seen at low tide. Distribution of small crabs was very patchy in this tidal environment, and it may be that this patchiness is the result of hermit crab life history patterns. Further investigations should examine the hermit crab life cycle in greater detail to explain small crab distribution patterns.

Preference trials. Difficulties with our perference trials need to be acknowledged. In an effort to sequester test subjects in an unfamiliar environment, we inadvertently left naive crabs in a large bucket under open sun before trials began. That sun exposure could have substantially influenced the choices made by our crabs, especially in the shade preference trials. Response to food may also have been influenced by recent feeding of crabs at high tide, and the shelter trials were likely affected by the presence of (even motionless) observers. In order to improve preference trial methodology for future studies, we suggest using a larger sample size of naive crabs that have not experienced heat stress, and making further efforts to minimize effect of nearby observers.

Given these experimental problems and biases, we nonetheless found strong preferences to habitat features in both large and medium size hermit crabs. Medium crabs showed a significant preference for the high tide litter over forest litter (T1-M, Table 1), whereas the latter was significantly preferred by large crabs. As this litter preference trial was not biased by heat stress or recent feeding of test subjects, we believe these results are good indicators of crab habitat preferences. Considered together with the crab distribution data, this finding further substantiates the specific habitat associations we found among the size classes of hermit crabs.

While the trial subjects may have been biased by experimental heat stress, there is other evidence that natural heat stress limits crab distribution. We observed that early in the morning (0800) hermit crabs of all size classes, but especially medium sizes, were more evenly distributed along the beach than later in the day as low tide approached. Rather than being near the high tide line where food forage was probably most available, many medium crabs appeared to be closer to the receding waters on bare sand. As the sun rose, crabs rapidly climbed the beach for the shelter of logs and leaves. Given these observations and the results of our shade trials (T2, T4, T5, and T6), we conclude that heat stress is probably the second most important factor (after the tidal cycle) determining hermit crab distribution.

Shelter seemed to play an important role in preference trials. Medium crabs in T6 appeared to use driftwood refuges for shade as well as shelter, crawling near but not under the thickest pieces of driftwood. Such strong shelter preferences, especially over food (T5-M, Table 1), seemed unusual for a hermit crab which relies on its lack of movement and cryptic shell to discourage predation. Again, our preference trials may have been biased toward shelter by either lack of subject's hunger or fear of observers. It seems likely that food resources are not limiting to hermit crabs in the forage-rich upper beach environment. As demonstrated by Burnaford et al. (1992), shell availability is more likely to influence intraspecific crab competition.

Taken together, our crab distribution data and preference trials indicate that hermit crabs exhibit specific habitat preferences at low tide. Hermit crabs also appear to be substantially influenced by heat stress and refuge needs. As both the forest and high tide habitats provide shade, food forage, and shelter, it appears that large and medium-sized hermit crabs may reduce intraspecific competition by partitioning resources in differently preferred upper beach habitats.

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